THE GENERA OF JUGLANDACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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JUGLANDACEAE A. Richard ex Kunth, Ann. Sci. Nat. 2: 343. 1824, "Juglandeae," nom. cons.

(WALNUT FAMILY)

Trees [rarely shrubs] mainly of temperate regions, the branchlets terete, the wood durable, often dark-colored. Leaves deciduous [or evergreen], alternate [or opposite], petiolate, imparipinnate, usually glandular-dotted beneath and aromatic, exstipulate. Flowers imperfect. Staminate flowers borne in pendulous [rarely erect] aments, 3- to several-fasciculate on branches of the previous year or at the base of branches of the year, or solitary and lateral [or borne in a terminal cluster of several pendulous or erect aments with a central carpellate ament]; each staminate flower with a primary bract,[2] 2 secondary bracts [sometimes absent], and 4 or fewer perianth lobes, or the perianth sometimes absent (*Carya*, *Platycarya*); stamens 3–100, attached to the receptacle and borne in 1 to several series, the filaments short, free, the anthers basifixed, erect, 2-locular, with longitudinal dehiscence, a rudimentary gynoecium occasionally present. Carpellate flowers borne [on a central ament in a terminal cluster of staminate aments or] on a solitary [pendulous to] erect, often few-flowered spike, each sessile flower composed of a floral envelope and gynoecium, the floral envelope consisting of an involucre composed of a

[1] Prepared for a generic flora of the southeastern United States, a project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB–6459X, principal investigator Carroll E. Wood, Jr.). This treatment follows the format established in the first paper of the series (Jour. Arnold Arb. **39**: 296–346. 1958). The area of the flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with additional information about extraterritorial taxa in brackets. References that I have not seen are marked by an asterisk.

I am grateful to Dr. Wood for his thorough editing, valuable suggestions in the course of this study, and the several weeks he devoted to the manuscript. Dr. Donald E. Stone has read the manuscript and has offered a number of useful and much-appreciated comments. Mrs. Nancy Dunkly has helped greatly in checking the bibliography and typing the manuscript. The illustrations are by Virginia Savage, largely from materials from the Arnold Arboretum supplemented by some preserved material of *Carya* kindly sent by Dr. Stone.

[2] The primary bract of *Alfaroa* and *Engelhardia* (*Engelhardtia*) is 3-lobed and is interpreted by Hjelmqvist (1948) as representing the fusion of two lateral secondary bracts with the primary bract.

primary bract [3-lobed in *Alfaroa* and *Engelhardia*] and 2 secondary bracts (occasionally modified or partly or wholly absent) and of a 4-parted perianth; primary and secondary bracts adnate at least to the base of the ovary, one or more perianth lobes occasionally modified or perianth absent (*Carya*); gynoecium syncarpous, usually of 2, rarely 3 or 4 carpels, the ovary inferior, 1-locular above, 2- or 4[8]-locular near the base, the single ovule erect, basal but at the apex of the incomplete septum(a), orthotropous, with a single integument; stigmas 2 (sometimes deeply 4-parted), sessile on the ovary, generally fleshy and papillate. Fruit drupaceous, a nut with a leathery or fibrous, dehiscent or indehiscent husk [3] [or fruit a nut with a wing or wings formed by the persistent primary and/or secondary bracts]; pericarp generally indurated, intrusive at the base, incompletely 2–4[8]-locular, the wall and septum(a) with or without longitudinal lacunae (cf. FIGURE 3, i, l). Seed large, filling the cavity of the pericarp, 2–4[8]-lobed; endosperm absent; seed coat thin; embryo oily, occasionally sweet, the large cotyledons variously lobed, twisted, or folded, the short radicle superior. Base chromosome number 16. TYPE GENUS: *Juglans* L.

A family of seven genera (eight if *Oreomunnea* Oersted is segregated from *Engelhardia* Leschen. ex Blume [4]), with approximately 60–65 species distributed primarily in temperate regions of the Northern Hemisphere but extending southward in montane areas of tropical America and Asia. The family is not known to be represented in either Africa or Australia, although *Engelhardia* reaches Java and New Guinea. *Platycarya* Sieb. & Zucc., *Pterocarya* Kunth, and *Cyclocarya* Iljinsk., are restricted to the Old World, *Alfaroa* Standl., is confined to the New, and *Engelhardia*, *Carya* Nutt., and *Juglans* L. are represented in both hemispheres (but see footnote 4). *Carya* and *Juglans* represent the family in the southeastern United States.

The family Juglandaceae is considered by Lawrence (1951) to comprise the monotypic order Juglandales, while Takhtajan (1969) includes the monotypic Rhoipteleaceae on the basis of the pinnately compound leaves and hard wood of *Rhoiptelea*, and Stone & Broome have found that the pollen ultrastructure of Juglandaceae and Rhoipteleaceae is compatible. Hutchinson (1967) and Cronquist (1968) include both families and the trifoliolate-leaved Picrodendraceae in the Juglandales. This order is closely allied with the Myricales, Betulales, and Fagales. The Juglandaceae are distinguished from other Juglandales by the unisexual flowers borne in catkins; the drupaceous or nut-like fruit; the solitary basal,

[3] The husk (incorrectly called "exocarp" by some authors) is derived from the involucre and the perianth, while the hard shell of the nut is derived from ovarian wall that becomes sclerified before maturity.

[4] Although *Oreomunnea* has traditionally been considered to be congeneric with *Engelhardia*, Stone (Ann. Missouri Bot. Gard., in press) has reëxamined the evidence and thinks that the two should be recognized as distinct genera. *Engelhardia* as then circumscribed is restricted to the Old World, *Oreomunnea* to the New.

orthotropous ovule with a single integument borne in a 1-locular, inferior ovary; and the pinnately compound, exstipulate leaves.

Pollen studies by Whitehead (1965) have shown that the family includes several types. On the basis of ten characters that presumably indicate evolutionary trends within the family (including increase in size, sphericity, presence of pseudocolpi, distinctness of the columellae, irregular thickening of the ektexine, increase in pore number, increase in heteropolarity, and various ektexinous thickenings) *Engelhardia Roxburghiana* Wall. is considered to have the least specialized pollen. Pollen of *Engelhardia* and of the somewhat more specialized *Alfaroa* is isopolar and triporate (occasionally tetraporate, rarely pentaporate). Pollen of *Platycarya* is also basically triporate (bi- to pentaporate) but the presence of arcuate pseudocolpi indicates increased specialization. Distinctly larger and definitely heteropolar, the pollen grains of *Carya* are generally triporate. The specialized grains found in *Juglans* and *Pterocarya* are large, stephanoporate to basically periporate, and heteropolar. In *Juglans* the pores may vary from 2 to 37 per grain, with 6 to 18 the prevailing numbers. According to Erdtman, the Juglandaceae have several pollen characters in common with the Betulaceae, Casuarinaceae, Myricaceae, and Rhoipteleaceae.

Studies of the secondary xylem have shown that of *Alfaroa* and *Engelhardia* to be the least specialized (Heimsch & Wetmore, 1939). The diffusely distributed vessels of *Alfaroa* have thin walls and the vessel elements have scalariform perforations. Although similar, the wood of *Engelhardia* appears to be more specialized in its ring porosity. *Juglans* and *Pterocarya* are closely allied in several common anatomical features, although *Juglans* appears to be slightly more specialized. Anatomically *Platycarya* is somewhat isolated, having attained a high degree of specialization in the inflorescence, while the wood is relatively unspecialized as in *Alfaroa* and *Engelhardia*. The greatest specialization in the secondary xylem, i.e., distinct ring porosity and rounded, thick-walled vessels, has been reached by *Carya*. Iljinskaya (1953) notes that *Cyclocarya* has ring-porous wood as in *Carya* and *Platycarya*. Since *Alfaroa* and *Engelhardia* exhibit less specialized wood structure than the Anacardiaceae, it seems improbable that the Juglandaceae were derived from the Anacardiaceae as suggested by Cronquist (1968).

From a morphological study of the inflorescences and flowers of the Juglandaceae, Manning (1938, 1941, 1948) concluded that *Carya* and *Juglans* are the most specialized and *Engelhardia* and *Alfaroa* the least specialized genera of the family. Evolutionary trends leading to the Juglandaceae apparently included the development of imperfect-flowered axillary catkins from a terminal, highly branched panicle of perfect flowers. In general, the reduction of floral parts in the Juglandaceae supports the conclusions drawn from pollen and anatomical studies.

Various authors have grouped the genera of Juglandaceae into two subfamilies on the basis of the fruit type (winged, nutlike fruits *vs.* unwinged, drupaceous ones), but this distinction appears to be an artificial one.

In addition, there also appears to be no validly published name available for the subfamily that does not include *Juglans* when such a division is made. The names Nuciferoideae and Drupoideae proposed by Koidzumi (Acta Phytotax. Geobot. 6: 10. 1937) are not based on those of genera; Oreomunnoideae Leroy (Mém. Mus. Hist. Nat. Paris Bot. II. 6: 86. 1955) was published without a Latin description and indication of the type; and the properly formed name Pterocaryoideae used by Melchior (A. Engler's Syllab. Pflanzenfam. ed. 12. 2: 42. 1964) in place of Nuciferoideae is also invalid since he neither gave a full and direct reference to Koidzumi's description (as required by ICBN, Art. 33) nor supplied a Latin description and a type.

The extant genera and species of Juglandaceae appear to be the remaining stocks of a once large and much more widespread family. If identifications of fossils are correct, the earliest records of Juglans are from the Middle to Upper Cretaceous. *Carya* has not been attributed to the Cretaceous, although it was abundant in the Tertiary and present in later times. Fossils of *Engelhardia* and *Platycarya* are also known, and several extinct genera have been described.

The Juglandaceae are of considerable economic importance for their excellent wood and nuts (*Juglans*, *Carya*, *q.v.*). Several species of *Pterocarya* and the handsome shrubby tree *Platycarya strobilacea* Sieb. & Zucc. are cultivated as ornamentals in the United States.

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KEY TO THE GENERA OF JUGLANDACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *trees with hard, dark-colored wood; leaves pinnately compound, exstipulate; leaflets usually glandular-dotted beneath; flowers imperfect, the plants monoecious; staminate flowers bracteate, in pendulous aments, with or without a perianth; carpellate flowers bracteate, solitary or in small clusters, or in few-flowered spikes; perianth present (sometimes modified) or absent; gynoecium bicarpellate, ovary 1-locular, the single orthotropous ovule erect, basal; fruit drupaceous with a slightly fleshy or fibrous dehiscent or indehiscent husk surrounding a one-seeded nut; seed large, bilobate, germination hypogeal.*

Branchlets with continuous pith; leaflets with involute vernation; staminate aments usually 3-fascicled; stamens to 8 or 10 per flower (usually 4); perianth absent; carpellate flowers without a perianth; fruit dehiscent or partially dehiscent, husk usually splitting into 4 valves, the nut usually smooth. ..... 1. *Carya.*

Branchlets with chambered pith; leaflets with conduplicate vernation; staminate aments solitary or in pairs, stamens to 40 per flower; perianth 3–6-lobed; carpellate flowers with a 4-lobed perianth; fruit with an indehiscent husk, the nut irregularly furrowed. ..... 2. *Juglans.*

1. **Carya** Nuttall, Gen. N. Am. Pl. **2**: 220. 1818, nom. cons.

Trees of varied woodland habitats, with smooth or exfoliating, aromatic, resinous, gray bark; heartwood hard, brown, sapwood pale; branchlets terete, tough, flexible, with continuous pith, the bud scales few and valvate or numerous and imbricate, the axillary buds[5] smaller than the terminal bud. Leaves few- to many-foliolate, often glandular dotted beneath, petiolate, leaf scar large, elevated, oblong or semiorbicular, often 3-lobed, emarginate; leaflets involute in vernation, usually ovate to obovate, generally acuminate at apex, mostly oblique at base, serrate [entire],

[5] Paired valvate prophylls, probably protective in function, completely inclose (except for a terminal pore) the inner portions of the axillary buds.

FIGURE 1. **Carya** section **Apocarya.** a–h, *C. cordiformis*: a, staminate flower, × 12; b, stamen, × 15; c, three-lobed primary bract subtending stamens, × 10; d, branchlet with two carpellate flowers, × 1 1/2; e, carpellate flower and involucre, × 8; f, mature fruit with involucre dehiscing — note winged margins of valves, × 1; g, mature nut, × 1; h, terminal branchlet in winter condition with lower part in longitudinal section to show homogeneous pith, × 1. i–l, *C. illinoënsis*: i, mature fruit with involucre, × 1; j, mature fruit with one involucral valve removed, × 1; k, seed, × 1; l, terminal branchlet, winter condition, × 1. m, n, *C. myristiciformis*: m, mature fruit with involucre dehiscing, × 1; n, mature nut, × 1. o, *C. aquatica*: mature fruit with one involucral valve removed.

often subcoriaceous, sessile to short-petiolulate, becoming bright yellow in the fall. Flowers vernal, usually appearing after leaves unfold. Staminate flowers borne in slender, pendulous aments, these occurring singly or 5–8 in fascicles in the axils of the leaves of the previous year (occasionally of the current year) or at the base of the inner scales of the terminal bud; each flower subtended by a persistent, lanceolate bract; perianth absent, the floral envelope usually 2(3)-lobed, consisting of one primary plus two secondary bracts, the primary one linear to lanceolate, free to

near the base and usually much longer than secondary bracts, secondary bracts ovate, rounded to acuminate at the apex, fused with the primary bract near the base; stamens 3–10(–15), 2- or 3-seriate, inserted on the slightly thickened receptacle-like inner and lower face of the floral envelope; the anthers ovate-oblong, emarginate or divided at the apex, yellow or red, generally pilose or hirsute, as long as or longer than their slender connectives, the filaments abbreviated, free; gynoecium absent. Carpellate flowers borne in 2–10-flowered spikes terminal on branches of the year; perianth absent, each flower surrounded by a 4-lobed slightly 4-ridged involucre that is villose and covered on the outer surface with yellow glandular scales that ± persist in fruit; involucre often unequally lobed, composed of a primary bract and a 3-lobed structure probably representing 3 secondary bracts. Gynoecium bicarpellate, 4-locular at base, 2- and then 1-locular above at level of ovule (cf. FIGURE 2, f–h); stigmas spreading, papillate, ± united at the base, often persistent. Fruit often ovoid, globose or pyriform, the involucre of varying thickness, becoming indurated at maturity, 4-valved, promptly or tardily dehiscent to the middle or to the base; nut usually oblong, obovate or subglobose, narrowed and usually rounded at base, with 2 abaxial sutures, each valve enclosing half of each cotyledon, usually smooth externally, variously ridged internally, 4-locular at the base, above becoming 2-locular (by an incomplete middle septum separating the basal parts of cotyledons) and then 1-locular. Seed usually filling the nut cavity; testa thin, membranaceous; embryo with large fleshy cotyledons, the cotyledons oily, sweet to bitter, 2-lobed to near midway, the lobes oblong, compressed, with various longitudinal grooves, ± concave on the inner surface; radicle short, superior. Base chromosome number 16. (*Hicorius* Raf., 1817, nom. rejic.; *Hicoria* Raf., 1838, orth. mut.; *Pecania* Dochnahl.) LECTOTYPE SPECIES: *C. tomentosa* (Poiret) Nutt. (*Juglans tomentosa* Poiret), *typ. cons.* (Ancient Greek name, *karya*, applied to *Juglans regia*.) — HICKORY.

A genus of 15 species mainly of temperate eastern North America and southeastern Asia, represented in the eastern United States and parts of adjoining Mexico by 11 species, absent from western North America, although present there during the Tertiary. Four species occur disjunctly in southeastern Asia. The determination of the species of *Carya* should be approached with caution, for in addition to occasional hybrids, considerable intraspecific variation has lead to the description of numerous varieties, most of which are without merit. Although fruiting collections are often necessary for accurate identification, careful floral analysis should yield valuable data for distinguishing the species and understanding their biology.

Section APOCARYA C. DC. (*Hicorius* subg. *Pacania* Raf., subg. *Drimocarya* Raf.; *Hicorius* § *Apohicoria* Dippel; *Carya* § *Pacania* (Raf.) Rehder) contains eight species disjunctly distributed between the eastern United States, Mexico, and Asia. The species comprising this section have 5–17 serrate, usually falcate leaflets, 4–6 valvate bud scales (buds pos-

sibly naked in *C. cathayensis*) that are hardly or not at all accrescent in spring, 3–8 (usually 4) stamens, a husk with the valves not keeled but frequently narrowly winged along the margins, and lacunose wall partitions in the nut. At least all of the American species of the section are diploids, $2n = 32$, whereas species of section CARYA are predominantly tetraploid (Stone, 1963).

Four species of sect. APOCARYA are found in the southeastern United States. An important component of the deciduous forest of the eastern United States, *Carya cordiformis* (Wangenh.) K. Koch, bitternut hickory, $2n = 32$, occurs from New Hampshire, southernmost Quebec, New York, and southern Ontario, west to Minnesota and southeastern Nebraska, and south to northwestern Florida, eastern Oklahoma, and eastern Texas (see Little, 1971, *map 112-E*). This species is characterized by scurfy-yellow overwintering buds, lanceolate to lanceolate-ovate, scarcely falcate leaflets that are pubescent beneath, and cylindric to compressed fruit with the valves of the husk narrowly four-winged above the middle. It occurs most commonly in moist sites and reaches its greatest height (over 30 m.) in the rich bottomlands of the lower Ohio River basin. Hybrids with *C. illinoënsis* (*C.* × *Brownii* Sarg.), *C. glabra* (*C.* × *Demareei* Palmer), and *C. ovata* (*C.* × *Laneyi* Sarg.) have been reported.

The bitternut hickory is allied to *Carya Palmeri* Manning, an endemic of Nuevo León, Tamaulipas, and San Luis Potosí, Mexico, that differs from *C. cordiformis* in having tight, smooth bark, in the 11 (9–13) occasionally falcate leaflets, in the more frequently hairy rachises and twigs, and in the glandular peltate scales on the undersurface of the leaflets. On the basis of similarities in leaf margins, stomata, trichomes, bracts protecting the axillary buds, and fruit, Stone (1962) demonstrated close relationships between *C. cordiformis* and *C. Palmeri* and the Asian *C. tonkinensis* and *C. cathayensis*. Stomatal guard-cell size indicates that *C. Palmeri* is a diploid (Stone, 1961).

Abundant only in Arkansas on high bottom-flats of the Mississippi River Delta, *Carya myristiciformis* (Michx. f.) Nutt. (*C. "myristicaeformis,"* orth. error), nutmeg hickory, $2n = 32$, is also found sparingly in scattered localities in eastern South Carolina, Alabama, and Mississippi, and in southeastern Oklahoma, Louisiana, and eastern Texas, as well as disjunctly in Nuevo León and Tamaulipas, Mexico (see Little, 1971, *map 116-E*). Often a tall tree (to ca. 35 m.), *C. myristiciformis* has a nut with a thick hard shell; ovate-lanceolate to broadly obovate, more or less falcate leaflets; and long-pedunculate staminate catkins borne at the base of branchlets of the year. This species is not known to form hybrids.

Largely restricted to bottomlands and swamps, *Carya aquatica* (Michx. f.) Nutt. (*Hicorius aquaticus* (Michx. f.) Britton), water hickory or bitter hickory, $2n = 32$, is found primarily on the Coastal Plain from southeastern Virginia and eastern North Carolina to southern Florida and eastern Texas, and in the Mississippi Embayment to southeastern Oklahoma, western Tennessee, southeastern Missouri and southern Illinois (see Little, 1971, *map 111-E*). The distinctive characters of this species include the

exfoliating bark, the reddish-brown, yellow-glandular overwintering buds, the lanceolate-falcate leaflets, and the laterally compressed nut with husk wings extending to the base. *Carya aquatica* is reported to hybridize with *C. texana* (*C.* × *ludoviciana* (Ashe) Little) and with *C. illinoënsis* (*C.* × *Lecontei* Little). In a study on the hybridity of *C.* × *Lecontei* by an examination of the fatty acids in the oil of the embryo, Stone, Adrouny & Adrouny found that the reputed hybrid contained amounts of fatty acids intermediate with the two probable parents.

The pecan, *Carya illinoënsis*[6] (Wangenh.) K. Koch (*C. olivaeformis* (Michx.) Nutt., *C. Pecan* (Marsh.) Engl. & Graebn., *Hicorius Pecan* (Marsh.) Britton), appears to be native to the Mississippi River Valley from southern Indiana, northern Illinois, and southeastern Iowa, to Alabama, Mississippi, Louisiana, and eastern Texas, but its original range is difficult to determine since it probably was spread by Indians, and it has been widely planted throughout most of the southeastern United States. It also occurs in scattered localities from Coahuila and Nuevo León, Mexico, southward to Jalisco, Hidalgo, and Oaxaca (see Little, 1971, *maps 114-W, 114-E, 114-N*). The combination of overwintering buds covered with clusters of yellow hairs; oblong-lanceolate leaflets, the lower pairs falcate; staminate catkins sessile or subsessile near the summit of shoots of the preceding year; and elongate fruits distinguishes the species. In addition to hybrids with *C. cordiformis* and *C. aquatica*, *C. illinoënsis* is reported to hybridize with *C. laciniosa* (*C.* × *Nussbaumeri* Sarg.) and with *C. tomentosa* (*C.* × *Schneckii* Sarg.), of sect. CARYA.

The remaining species of sect. APOCARYA are Asiatic. *Carya cathayensis* Sarg. has been reported from Chekiang, Kweichow, and Kiangsi provinces, China. The closely related *C. tonkinensis* Lecomte has been collected in Yunnan, China; Tonkin, North Viet Nam; and Assam, India. *Carya Poilanei* (A. Chev.) Leroy is also known from Tonkin and from Laos. The only other Asiatic species of *Carya*, *C. sinensis* Dode, has been segregated from sect. APOCARYA to form the monotypic sect. RHAMPHOCARYA Manning & Hjelmqvist (*Annamocarya* A. Chev.), mainly on the basis of its 7–9 entire leaflets, either hollow or solid pith, few and unequal bud scales, staminate catkins in fascicles of five to eight, 5–15 stamens, 4–6 apically keeled valves of the husk, and lacunae absent in the lower part of the walls of the nut but sometimes present near the apex.

The New World section CARYA (*Carya* § *Eucarya* C. DC.; *Hicorius* subgen. *Glycaria* Raf., subgen. *Hexacarya* Raf.; *Hicorius* § *Euhicorius* Dippel, § *Eucarya* (C. DC.) Sarg.) contains seven species of the eastern United States and northeastern Mexico. Species of this section have 3–9 serrate, nonfalcate leaflets; 6–12 imbricate bud scales that are strongly accrescent in spring; 3–8, but usually 4, stamens; a 4-valved husk with the valves neither strongly keeled nor winged along the margin; and wall

[6] According to Thieret (1961) the original, and consequently correct, spelling of the epithet is *illinoinensis*. The Standing Committee on Stabilization appointed by the XI International Botanical Congress (1969) has ruled, however, that *illinoinensis* is an orthographic error and the spelling *illinoënsis* should be retained.

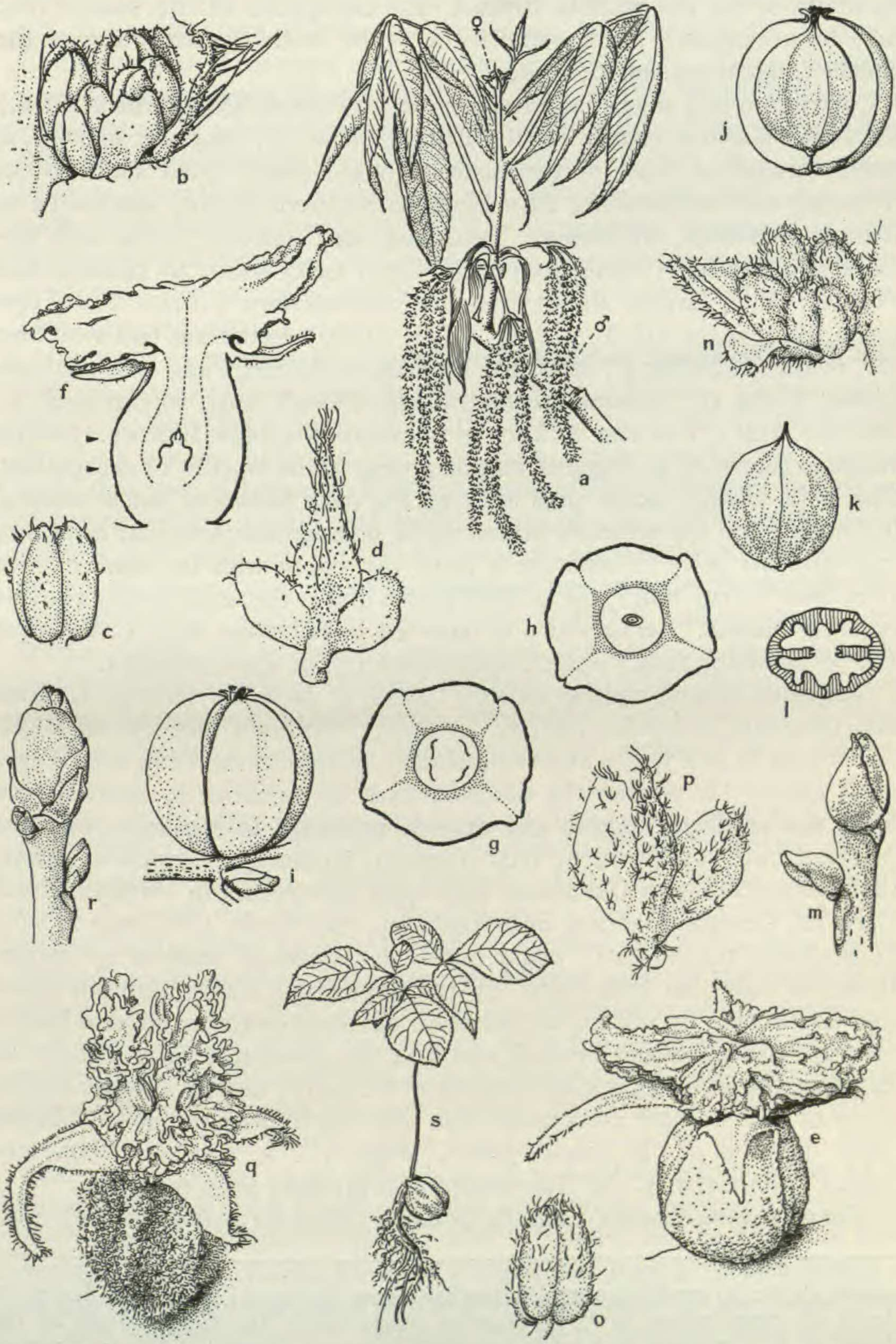

FIGURE 2. **Carya** section **Carya.** a–m, *C. ovata* var. *australis*: a, flowering branchlet with staminate and carpellate inflorescences, × 1/3; b, staminate flower, × 10; c, stamen, × 12; d, bracts subtending staminate flower, × 10; e, carpellate flower, × 6; f, semidiagrammatic longitudinal section of carpellate flower showing ovule, × 6; g, semidiagrammatic basal cross section of carpellate flower (at level of lower arrow in "f"), showing four-loculate condition of

partitions of the nut without lacunae. All the species of this section that have been examined are tetraploid, $2n = 64$, with the exception of the diploid *C. laciniosa* and *C. ovata*.

Common in rich woods, bottomlands, and on slopes, *Carya ovata* (Mill.) K. Koch (*Hicorius ovatus* (Mill.) Britt.), $2n = 32$, shagbark hickory, is found throughout most of the eastern United States from southeastern Nebraska and southeastern Minnesota to southern Maine, southward to Georgia, Alabama, Mississippi, Louisiana, and eastern Texas, and disjunctly in Mexico (Tamaulipas and Nuevo León south to Hidalgo and Puebla). It is largely absent from the southeastern Coastal Plain (see Little, 1971, *maps 118-N, 118-E*). Little (1969) recognizes two varieties: var. *ovata* (including *C. mexicana* Engelm. ex Hemsl.) and var. *australis* (Ashe) Little (*C. carolinae-septentrionalis* (Ashe) Engl. & Graebner, *C. australis* Ashe), Carolina hickory or southern shagbark hickory. Several varieties described by Sargent do not appear to be worthy of recognition. The fruits usually longer than 3.5 cm., the dark brown or black terminal bud scales, and the generally lanceolate or oblanceolate terminal leaflets of var. *australis* serve to separate it from var. *ovata* with its smaller fruits (less than 3.5 cm. long), tan or light brown bud scales, and usually obovate terminal leaflets. *Carya ovata* is reported to hybridize with *C. laciniosa* (*C.* × *Dunbarii* Sarg.) and *C. cordiformis* (*C.* × *Laneyi* Sarg.).

The other diploid member of sect. CARYA, *C. laciniosa* (Michx. f.) Loudon (*Hicorius laciniosus* (Michx. f.) Sarg.), shellbark hickory, $2n = 32$, is common in rich woods and bottomlands, mainly in the Ohio and Mississippi valleys. It reaches the northern limit of its range in western New York and southern Ontario and extends westward to southern Iowa and Missouri, and southward to West Virginia, Kentucky, Tennessee, Arkansas, and northeastern Oklahoma, with local occurrences in Virginia, North Carolina, Georgia, Alabama, and Mississippi (see Little, 1971, *map 115-E*). It is closely related to *C. ovata* but is distinguished from it by orange-brown or light tan branchlets; by the larger bud scales, glabrous above and accrescent; by oblong-lanceolate to oblong-obovate acuminate leaflets that are soft-pubescent beneath and lack the prominent tufts of hairs located on the serrate margins of leaves of *C. ovata*; and by a large, angled, more or less strongly compressed nut with a yellowish- to reddish-brown shell. Hybrids of this species with *C. ovata* (*C.* × *Dunbarii* Sarg.) and with *C. illinoënsis* (*C.* × *Nussbaumeri* Sarg.) have been reported.

Carya pallida (Ashe) Engl. & Graebn. (*Hicorius pallidus* Ashe), sand

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ovary, × 8; h, semidiagrammatic median cross section of carpellate flower (at level of upper arrow in "f"), showing ovule filling the single locule at this level, × 8; i, mature fruit with involucre beginning to split, × 3/4; j, mature fruit with two involucral lobes removed, × 3/4; k, nut, × 3/4; l, median cross section of nut — cotyledons of embryo white, sclerified wall of nut hatched, × 3/4; m, terminal bud, winter condition, × 1. n–s, *C. laciniosa*: n, staminate flower, × 10; o, stamen, × 12; p, bracts subtending staminate flower, × 10; q, carpellate flower, × 6; r, terminal bud, winter condition, × 1; s, young seedling, × 1/6.

hickory, is largely confined to the Coastal Plain from southern New Jersey to northwestern Florida and Louisiana, and north in the Mississippi Embayment to Tennessee and southeastern Kentucky. Deam (1940) reported it from Knox County, Indiana. It is readily distinguished by the combination of silvery-lepidote overwintering buds and staminate inflorescences; long-attenuate resinous and aromatic leaflets that are silvery-lepidote beneath when expanding; and yellow-lepidote husk that tardily splits to the base (Fernald, 1950). The chromosome number of *C. pallida* has not been determined, but on the basis of stomatal guard-cell size it is presumed to be tetraploid (cf. Stone, 1961). No hybrids with other species have been reported.

Common in most of the eastern United States, generally in dry woods and on slopes, *Carya glabra* (Mill.) Sweet (*Hicorius glabrus* (Mill.) Britt.; *C. leiodermis* Sarg., cf. Little, 1969), $2n = 64$, is characterized by close, usually furrowed and rigid bark; acute overwintering terminal buds that are glabrous at first but become silky pubescent in autumn; glabrous petioles, rachis, and leaflets; and obovoid, dark brown, smooth, shining fruit with the husk indehiscent or opening tardily by only one or two sutures. Little (1969) recognized two varieties in this species in addition to var. *glabra* (*C. microcarpa* Nutt., *H. microcarpus* (Nutt.) Britt.), which occurs from Massachusetts and southern New Hampshire to New York, southern Ontario, southern Michigan, Illinois, and northeastern Kansas, south to Arkansas, Mississippi, Georgia and northwestern Florida. Varietas *megacarpa* (Sarg.) Sarg. (*C. Ashei* (Sudw.) Kelsey & Dayton, *H. austrinus* Small, *C. austrina* (Small) Murrill), coast pignut hickory, with larger leaflets and fruits, is found from western New York to southern Ohio and Illinois, south to eastern Texas, Louisiana, and central Florida. Varietas *odorata* (Marsh.) Little (*C. ovalis* (Wangenh.) Sarg., *C. ovalis* var. *odorata* (Marsh.) Sarg.), red hickory, with a smaller globose or pyriform fruit, the husk of which splits to the base by four sutures, is of scattered occurrence throughout most of the range of var. *glabra*. (See Little, 1971, *map 113-E*, for distribution of the species.)

A small tree or shrub confined to the scrub of dry sand-ridges from central to northwestern Florida, *Carya floridana* Sarg. (*Hicorius floridanus* (Sarg.) Small), Florida or scrub hickory, $2n = 64$, is closely related to *C. glabra*, which in Florida occurs largely in hammocks, and to *C. texana*, which has a similar rusty pubescence of undulating peltate scales on the young leaves. Kurz & Godfrey (1962) question the taxonomic distinctness of *C. floridana*, since intergrades with *C. glabra* can be found in intermediate habitats. *Carya floridana* is separated from *C. glabra* largely by its habitat and by the characteristic rusty pubescence of the young leaves.

Carya texana Buckl. (*C. Buckleyi* Durand, *C. villosa* (Sarg.) Schneider, *C. arkansana* Sarg.), black hickory, $2n = 64$, occurs from eastern Kansas, Missouri, southern Illinois, and southern Indiana to eastern Oklahoma, central Texas, and southern Louisiana. Related to both *C. ovata* and *C. floridana*, *C. texana* typically has rusty-pubescent young branchlets and overwintering buds, bud scales hairy-tufted at the apex, leaflets rusty-

pubescent beneath with peltate scales, and yellow-scurfy fruit with the husk splitting either to the middle or nearly to the base. This species appears to be restricted to dry upland woods or dry sandy or rocky slopes. A hybrid between *C. texana* and the bottomland diploid *C. aquatica* (*C.* × *ludoviciana* (Ashe) Little) has been reported, but according to Little (1953) additional study is needed to determine its true identity. Laughlin has described a hybrid between *C. texana* and *C. tomentosa* (*C.* × *collina* Laughlin).

A woodland species, *Carya tomentosa* (Poiret) Nutt. (*C. alba* (Mill.) K. Koch non (L.) Nutt. ex Ell., nom. ambig.), mockernut hickory, $2n = 64$, is found from New Hampshire, southernmost Ontario, southern Michigan, and southeastern Iowa, south to northern Florida and eastern Texas (see Little, 1971, *map 117-E*). *Carya tomentosa* is separated from the phenotypically similar *C. laciniosa* and *C. ovata* by its tomentose branchlets, petioles, rachises, and lower leaf surfaces, with the trichomes usually being curly and fasciculate; by the outer bud scales deciduous in autumn, thus exposing the inner silky scales; by a husk that splits to or below the middle; and by the deeply furrowed but not exfoliating bark. In Illinois and Iowa it is known to hybridize with *C. illinoënsis* (*C.* × *Schneckii* Sarg.).

Most speculations about phylogenetic relationships within *Carya* have had to rely on morphological observations, but an analysis of the oils from the seeds of the different species has provided some additional insights into interspecific alliances. Stone, Adrouny & Adrouny (1969) found oils from members of sect. APOCARYA to have high oleic and low linoleic content, while species of sect. CARYA have a low ratio of oleic to linoleic acid. Ties between the two sections are found in the average oleic and linoleic acid values of *C. myristiciformis* and *C. aquatica*, of sect. APOCARYA, and *C. ovata* var. *australis* (*C. carolinae-septentrionalis*) and *C. laciniosa*, both diploids of sect. CARYA. Oil data also link *C. ovalis* with *C. aquatica*, *C. myristiciformis*, *C. laciniosa*, and *C. ovata*, although *C. ovalis* has traditionally been considered allied to *C. glabra*, and Little recently (1969) reduced *C. ovalis* to a variety (*odorata*) of *C. glabra*. The data support the close assemblage of *C. floridana*, *C. texana*, *C. tomentosa*, *C. pallida*, and *C. glabra*, and within this group of tetraploids, *C. floridana* and *C. texana* appear to be closely allied. A somewhat distant relationship was established between *C. illinoënsis* and *C. cordiformis*. Although it was impossible to test the oils from any of the Asiatic species, it was suggested that ties with them might be via *C. myristiciformis* and *C. aquatica*.

A perianth is considered by morphologists to be lacking in carpellate flowers of *Carya*, and the four structures surrounding the gynoecium are considered to represent involucral bracts. Manning (1941) has designated the lower or united basal part of the two stigmas as a "stigmatic disk," which represents a modified calyx, but he has not published supporting anatomical evidence. Developmental and detailed anatomical studies should be helpful in determining the nature of the accessory structures of the carpellate flowers.

Flowering of *Carya* species occurs in the spring (usually in April and May) with the enormous amounts of pollen being dispersed by wind. In a study of commercial cultivars of *C. illinoënsis*, J. G. Woodroof (1930) found that 26 were proterandrous, 18 proterogynous, and 88 homogamous. Warm, sunny days were found to be optimal for pollen shedding, high humidity or rain retarding or completely stopping anther dehiscence. In *C. illinoënsis* the Polygonum-type embryo sac is at the four-celled stage at the time of pollination. Fertilization apparently does not occur for five to seven weeks following pollination, although Shuhart (1932) reported only a two-week lag. Embryogeny in *C. glabra* is of the Asterad type.

Pollination studies of *Carya illinoënsis* have shown it to be capable of both self- and cross-pollination. Following self-pollination, however, a greater number of immature nuts are dropped, resulting in smaller yields of harvested nuts than from the cross-pollinated trees. The staminate inflorescences are differentiated during the summer and mature the following spring, while carpellate inflorescences apparently do not differentiate until late winter or early spring. Throughout much of the south-central United States, *C. illinoënsis*, a prodigious pollen producer, is a major factor in many spring pollen allergies.

The pollen grains of *Carya* are tectate, usually triporate, suboblate, rounded-triangular to circular in polar view, with finely scabrate sculpturing. They are distinctly heteropolar, the pores being slightly off the equator of the grain and the aperture $\pm$ circular in outline (Whitehead, 1965). It appears from pollen morphological relationships that sect. CARYA is derived from sect. APOCARYA. Stone (1963) pointed out that most species belonging to sect. APOCARYA (all diploids) have pollen grains smaller than 46 μ, while species of sect. CARYA (mainly tetraploids) have pollen grains larger than 46 μ. There is also a positive correlation between stomatal size and ploidy level.

Species of *Carya* were widespread (pantemperate?) during favorable climates of the Tertiary. Fossils of *Carya* of Eocene and Miocene age are known from Alaska, the western and northwestern United States, Vermont, the southeastern United States, Greenland, Iceland, Spitzbergen, Central Europe, Russia (Kamchatka), and China (Shantung). There are apparently no good Cretaceous records.

Several species of *Carya* (*C. ovata*, *C. laciniosa*, *C. tomentosa*, and *C. glabra*) are the main sources of hickory lumber. The seeds of most species of *Carya* are high in tannins and consequently are not used as a food source, although they are an important food for wildlife. Nuts produced by *Carya ovata* and *C. laciniosa* are reported to be sweet, edible, and of good quality. The pecan, obtained from *C. illinoënsis*, has become one of the world's important nut crops. Interest in commercial pecan growing, largely in the early 1900's, has resulted in the description of numerous horticultural varieties. These cultivars, many of them originally selections from native stands of *C. illinoënsis* but later from selective crossing, have formed the basis of the pecan industry of the southeastern and south-

central United States. Grown best on deep, loose, well-drained, well-aërated soil, *C. illinoënsis* can properly be considered a multipurpose species. The trees provide food for man as well as wildlife, they are suitable for landscaping, and the wood is widely used in the manufacture of tools, lumber, and veneers. The seeds are high in caloric value and have large amounts of unsaturated oils (ca. 72 per cent), protein (ca. 11 per cent), and carbohydrates (ca. 13 per cent).

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2. **Juglans** Linnaeus, Sp. Pl. 2: 997. 1753; Gen. Pl. ed. 5. 431. 1754.

Aromatic, resinous trees of temperate or subtropical habitats; bark furrowed, scaly; wood durable, dark-colored; branchlets terete, stout, with

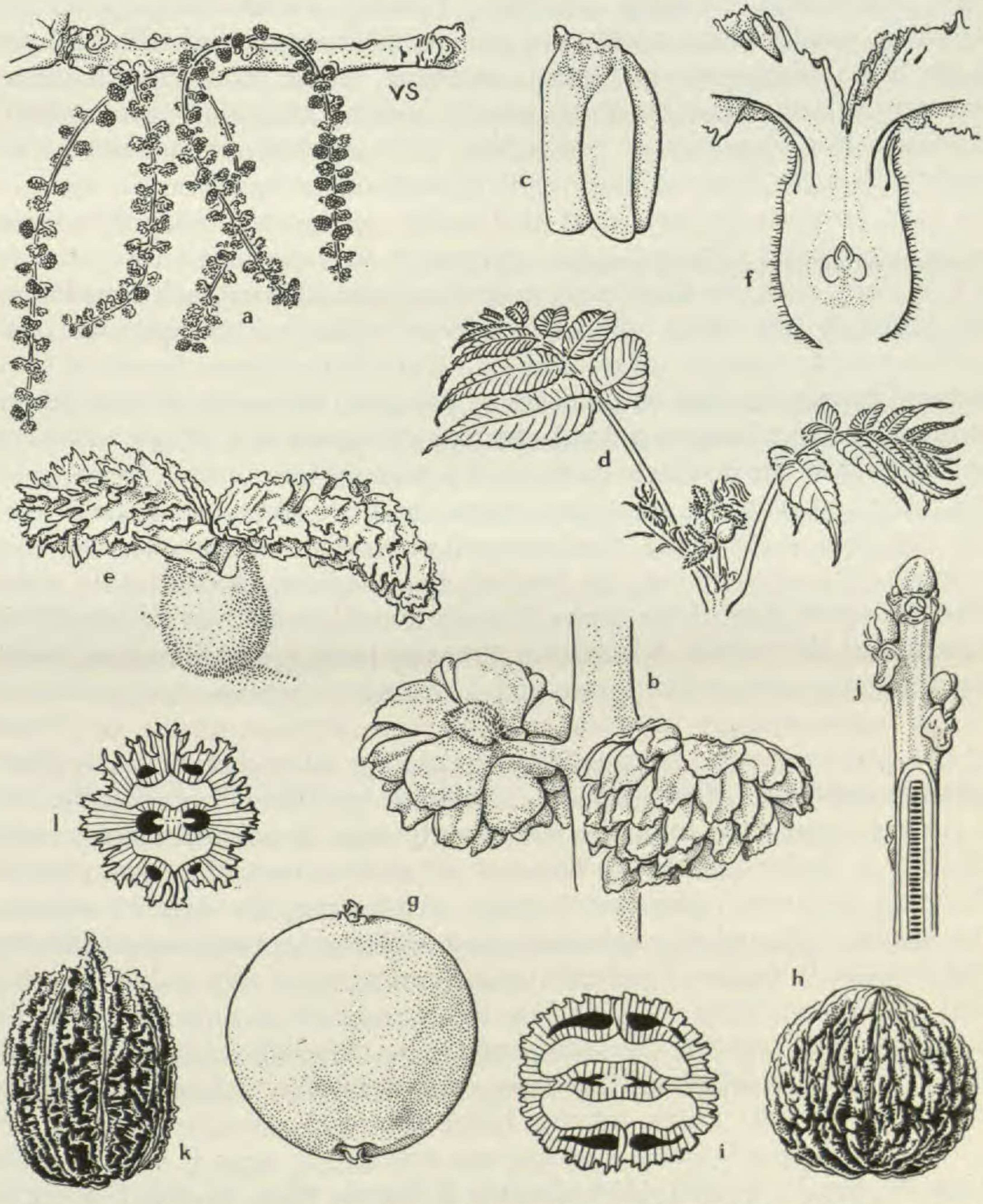

FIGURE 3. **Juglans.** a–j, *J. nigra*: a, branchlet with staminate inflorescences, × 1/2; b, part of inflorescence showing two staminate flowers and subtending bracts oriented as in "a", × 6; c, stamen, × 15; d, branchlet with terminal carpellate inflorescence, × 1/2; e, carpellate flower, × 3; f, semidiagrammatic longitudinal section of carpellate flower showing ovule, perianth, and involucre, × 4; g, mature fruit with indehiscent involucre, × 3/4; h, mature nut, × 3/4; i, median cross section of nut, cotyledons unshaded, lacunae in wall and septum black, × 3/4; j, terminal branchlet in winter condition with lower part in longitudinal section to show chambered pith, × 1. k, l, *J. cinerea*: k, mature nut without involucre, × 3/4; l, median cross section of nut, cotyledons unshaded, lacunae black, × 3/4.

chambered pith; terminal buds short to long, usually with 2 pairs of opposite scales, the inner scales accrescent, the axillary buds ± flattened, with 4 ovate scales. Leaves rarely paripinnate, few- to many-foliolate; petioles terete, canaliculate above, often swollen basally, the leaf scars large, conspicuous, elevated, obcordate, 3-lobed; leaflets conduplicate in vernation, usually ovate, acute to acuminate at the apex, generally oblique at the base, membranaceous, serrate or entire, sessile to short-petiolulate, pinnately veined. Flowers vernal, usually opening after the leaves unfold. Staminate flowers sessile or pedicellate, in many-flowered aments borne singly or in pairs from the lower axillary buds of the upper nodes, appearing from between the persistent bud scales; perianth 3–6-lobed, adnate to the ovate bract (FIGURE 3, b); stamens 8–40, inserted on the perianth in 2 to many rows, the alternately ranked stamens alternate with the lobes, the filaments free, short, the anthers erect, oblong, a conspicuous connective usually present; ovary lacking. Carpellate flowers borne in few-flowered terminal spikes on branches of the year, the ovary of each flower inclosed by and adnate to a floral envelope composed of a villous involucre and a perianth, the involucre made up of a primary bract (often free to near the base or fused to the secondary bracts) and two secondary bracts (usually free only at the apex), the bracts often laciniate at the apex, the four perianth lobes longer than the lobes of the involucre, appearing to come from the upper part of the ovary. Gynoecium 2(rarely 3 or 4)-carpellate, 1-locular at the middle, 4-locular at the very base, a major septum dividing the lower part of the locule and a secondary septum (perpendicular to the major septum) bisecting each of these divisions at the very base of the ovarian cavity; stigmas large, spreading, often clavate, fleshy, fimbriately papillate. Fruit globose, ovoid, or pyriform, occasionally obscurely 4-angled, the husk (formed mainly from involucral tissue) indehiscent, ± fleshy, glabrate to hirsute; nut globose to ovoid, often slightly flattened, indurated (the wall formed mainly from the ovarian wall, in our species thick and with lacunae in both wall and septum), longitudinally and irregularly rugose, 2-valved (upon germination), each valve inclosing half of each cotyledon, ± ribbed on the one or both sutures. Seed with a thin seed coat covering the large embryo, ± laterally compressed, shallowly or deeply lobed at the base, each cotyledon 2-lobed, filling the cavity of the nut; hilum minute, basal. Basic chromosome number 16. (*Wallia* Alef., *Regia* Loud.) LECTOTYPE SPECIES: *J. regia* L.; see Nuttall, Gen. N. Am. Pl. 2: 220. 1818; Britton & Brown, Illus. Fl. No. U.S. ed. 2. 1: 578. 1913. (Classical Latin name for walnut, *Juglans regia*, derived from *Jovis*, of Jove or Jupiter, plus *glans*, acorn.)

A genus of 18 to 20 species of temperate and subtropical regions of Europe, Asia, and the Americas. Six species are known from the United States; of these, the two in our area, *Juglans nigra* L. and *J. cinerea* L., are the only important forest species. *Juglans Hindsii* R. E. Sm. and *J. californica* S. Wats., $2n = 32$, are Californian (central California and coastal southern California respectively), while *J. major* (Torr. ex Sitzgr.)

Heller occurs from central and southwestern Texas to southwestern New Mexico and central Arizona and (as var. *glabrata* Manning) south to Guerrero, Mexico, and *J. microcarpa* Berl., $2n = 32$, ranges from western Oklahoma and western and southern Texas to northeastern Mexico. Manning (1957, 1962) also recognizes *J. pyriformis* Liebm., *J. hirsuta* Manning, and *J. mollis* Engelm. in Mexico. *Juglans Steyermarkii* Manning is endemic to Guatemala, and *J. olanchana* Standl. & Williams extends from Nicaragua to Guatemala with a disjunction (var. *Standleyi* Manning) in Colima and Jalisco, Mexico. The misnamed *J. jamaicensis* C. DC., $2n = 32$, occurs in Cuba, Hispaniola, and Puerto Rico. *Juglans* recurs in the Andes with some five species distributed from Colombia and Venezuela south to Peru, Bolivia, and Argentina. *Juglans regia* L. is native from southeastern Europe to India (and perhaps Central Asia) but is widely planted in many other temperate climates of the world. *Juglans cathayensis* Dode, *J. cordiformis* Maxim. (including *J. ailantifolia* Carr., *J. Sieboldiana* Maxim. non Göppert), $2n = 32$, *J. mandschurica* Maxim., $2n = 32$, and *J. stenocarpa* Maxim. represent the genus in eastern Asia.

In the subgeneric classification proposed by Dode (1909), who recognized many more species, *Juglans regia* constitutes sect. JUGLANS (§ *Dioscaryon* Dode), and *J. cinerea* is alone in sect. TRACHYCARYON Dode. All of the other Old World species are placed in sect. CARDIOCARYON Dode and the other New World ones in sect. RHYSOCARYON Dode.

The black walnut, *Juglans nigra* L. (*Wallia nigra* (L.) Alef.), $2n = 32$, occurs from western Massachusetts, central Vermont, and southern Ontario to southern Minnesota and southeastern South Dakota, south through eastern Nebraska to western Oklahoma and eastern Texas, and to northwestern Florida and Georgia (see Little, 1971, *map 134-E*). A plant of low altitudes, *J. nigra* grows best on deep well-drained soils, including good bottomlands. It can be found in mixed mesic forest, but rarely in pure stands. This species is easily distinguished by the lower surface of the leaflets and petioles being minutely downy with solitary or paired hairs, by the notched leaf scars that lack a fringe of hairs, and by the spherical fruit. Varietas *oblonga* (Marsh.) Fern. differs only in having ellipsoidal fruits. Flowering in early spring as the leaves appear or slightly afterward, the trees are apparently self-fertile, but individual trees have varying degrees of proterandry or proterogyny. Cross pollination usually insures better seed set and higher fruit yields.

Distributed over much of the northeastern United States, *Juglans cinerea* L. (*Wallia cinerea* (L.) Alef.), butternut, $2n = 32$, occurs from western New Brunswick, New England, southern Quebec, and southern Ontario to Wisconsin and Minnesota, south to northern New Jersey, Virginia, North Carolina, northwestern South Carolina, northern Georgia, Alabama, and Mississippi, Arkansas, and Missouri (see Little, 1971, *map 133-E*). Apparently growing best on streambanks and on well-drained gravelly or rocky soils, this species, like *J. nigra*, occurs sparingly throughout its range. It is found in many mesic forests, but it is better adapted to limestone soils than *J. nigra* is. *Juglans cinerea* is characterized by its

leaflets, downy with fascicled hairs, especially beneath; by the branchlets and petiole downy with glandular hairs; by the leaf scars with a hairy fringe along the upper margin; and by the ellipsoidal fruit.

Juglans appears to be a homoploid genus with $2n = 32$ (eleven species). *Juglans nigra* and *J. cinerea* are not known to hybridize, but hybrids of *J. nigra* with *J. Hindsii* and *J. regia* and of *J. cinerea* with *J. cordiformis* and *J. regia* have occurred under cultivation or have been produced artificially. Hybrids of *J. regia* with *J. Hindsii* and *J. cordiformis* are also known.

The characteristic chambering of the pith in *Juglans* was shown by Harlow (1930) in *J. nigra* and *J. cinerea* to be formed at the end of the growing season. In spring the young twigs of the year still have homogeneous pith. Chambering in *J. nigra* begins in late August, but in *J. cinerea* not until late September or early October. The first sign of chambering is a change in the color of the pith, followed by the formation of several cavities near the base of the year's growth (after elongation has ceased) and then throughout the twig.

Both prodigious pollen producers, *J. nigra* and *J. cinerea* were suspected of contributing to spring pollen allergies, but since neither occurs abundantly anywhere, it is doubtful that either is of importance in this connection. The pollen grains are 2-celled when shed. The pollen is relatively variable but is basically tectate, periporate, and heteropolar with the (2–)6–18(–37) pores restricted to one polar hemisphere and occasionally overlapping (Whitehead, 1965). An increase in pollen size and in pore number, as seen in *J. regia* and *J. nigra* may be indicative of specialization within the genus.

Unlike genera of the Fagaceae and Betulaceae, in *Juglans* the ovule is well developed at the time of pollination, with fertilization occurring 4–8 days later. Nuclear endosperm has been reported in *J. regia* (Nast, 1935, 1941) with approximately 1000 free nuclei present before cell wall formation occurs. Embryogeny in *J. mandschurica* is of the Asterad type (Langdon, 1934). Polyembryony has been reported in *J. nigra*.

After flowering the fruits of our species mature in September or October of the same season, dropping shortly after the leaves fall. Hypogeous germination usually occurs the following spring with a strong taproot produced by the seedling.

Although Berry (1923) suggested that *Juglans* leaves have been found in Middle Cretaceous deposits, verifiable remains occur only from the Upper Cretaceous to the present. Apparently *Juglans* was much more widely distributed over the Northern Hemisphere in the past, especially during the Eocene, Miocene, and Pliocene.

It has long been known that certain plant species have reduced growth rates and/or reduced reproductive success when growing under or close to plants of certain species of *Juglans*, e.g., *J. nigra* and *J. regia*, but not *J. cinerea*. The inhibitory substance produced by these species has been determined to be juglone, $C_{10}H_6O_2$, a red crystalline compound, that is produced by oxidation of hydrojuglone, a water soluble substance pro-

duced in the leaves, fruit, husk, bark, and perhaps the roots. This substance apparently can be washed from the leaves into the ground by rain. This general phenomenon, allelopathy, the inhibition of one plant by a substance or substances secreted by another has only relatively recently received serious attention from ecologists (cf. Muller, 1969). Other examples have been discovered in several unrelated families, including the Gramineae, Simaroubaceae, Myrtaceae, Labiatae, and Compositae.

The beautifully grained brownish wood of *Juglans nigra* is perhaps the foremost cabinet wood of North America; that of *J. cinerea* is considered to be less valuable. Selected strains and cultivars of *J. nigra* (more than 100) have been developed, mostly for nuts with larger, thinner shells that will crack easily and for low seed-abortion rates. The seeds are used largely in ice cream and confectionery and as a flavoring. The nuts of *J. cinerea* are occasionally used locally but are not commercially important. A few cultivars, based on foliage characters, have been selected as ornamentals. The European *J. regia* is the principal source of walnut lumber and nuts in the Old World. It is successfully grown in various parts of the United States and is extensively cultivated in the mild climates of California.

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